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# SEASONAL DURATION OF ASCOSPORE EXPULSION OF ENDOTHIA PARASITICA*

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The effect of moisture upon the expulsion of ascospores of the chestnut blight fungus, *Endothia parasitica* (Murr.) And., was first studied by Rankin (1). Later the same writer (2) made the following report: "The speaker found the ascospores being shot from mature pustules during every rainy period last summer" (1911). A more detailed study of ascospore expulsion was made during the following summer by Anderson and Babcock (3). The main conclusion of these writers on the moisture relation can best be presented in their own words: "We may say then in general that, as long after a rain as the surface of the bark remains wet, the spores will continue to shoot."

That certain temperature conditions must be fulfilled to insure spore expulsion was first brought out by laboratory tests reported by the senior author (4). Later in a discussion of "The relative prevalence of pycnospores and ascospores of the chestnut blight fungus during the winter," Heald and Gardner (5) report the results of field tests made during the winter of 1912–13, showing that ascospores were not expelled during the warm winter rains. A brief statement of the relation of temperature to the expulsion of ascospores of *Endothia parasitica* has been published by Walton (6) and a more detailed consideration by Heald and Walton (7) of the temperature relation based on laboratory tests in constant temperature rooms has substantiated the earlier results. The only previous work bearing on the seasonal duration of ascospore expulsion is that of Rankin to

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* During the first part of the period covered by this paper, Mr. M. W. Gardner was associated with the writers, and he deserves special mention for careful and painstaking work in connection with the records and observations made at West Chester.

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which reference has been made, and observations made by Anderson and Babcock (3) during every rain period for the month of August, 1912.

It seemed desirable to have continuous records of the behavior of definite groups of perithecial pustules through one or more seasons under natural field conditions. For this purpose the work presented in the following pages was undertaken.

## METHOD AND PLAN

In carrying out this work the first requisite was a means of holding a glass slide over a definite area of perithecia-bearing bark. For this purpose a wooden bracket was devised. This is a small rectangular block, the width of an object slide, carrying a slot at one end for the insertion of the slide, and attached to the tree by a brass screw passing through the center (Fig. 1). On some trees the bracket was directed downwards, in which case the object slide was held in position by a screw turned into the bark (Fig. 1, *A*). In both cases the object slide was always wedged firmly into the slot. Ascospore

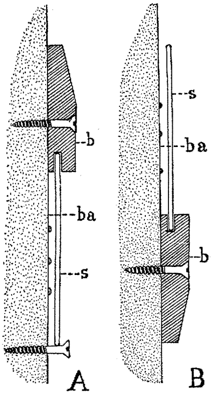

FIG. 1.

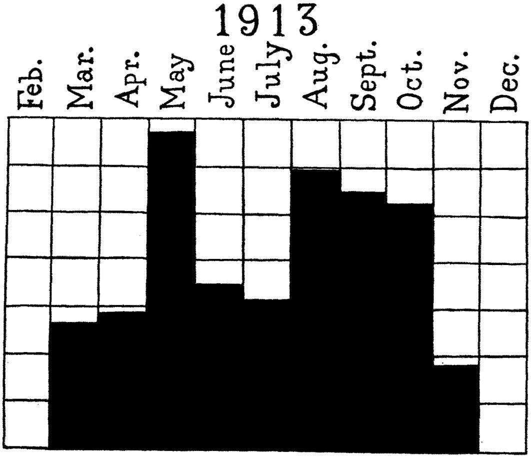

FIG. 2.

FIG. 1. Diagram of ascospore traps, showing the two positions employed; *b*, bracket; *ba*, bark bearing perithecial pustules; *s*, object slide for catching the expelled spores.

FIG. 2. Diagram showing the relative intensity of ascospore expulsion at West Chester, Pa., during the season of 1913.

expulsion was recorded equally well by slides in either position. Form *A* was designed to prevent excessive washing of the slide by the rain, while form *B* allowed a more ready penetration of the water. This device has been designated as an "ascospore trap" to distinguish it from other kinds of spore-traps (5, 8).

The original plan called for the placing of sets of ascospore traps on typical lesions under three different field conditions: first, in young chestnut coppice; second, in a chestnut orchard; third, in a forest. Owing to lack of assistance it was necessary to omit the traps from forest trees. A suitable chestnut coppice was found near West Chester, Pa., and the orchard of the Paragon Fruit and Nut Co., Martic Forge, Pa., was selected for the second set of traps. A set of standard weather instruments, including a rain gauge, Friez thermograph, and Friez hygrograph was installed at each station. Following each rain or rain period the slides were collected and brought to the laboratory and a record made of the amount of ascospore expulsion shown for each trap.

## THE TRAPS AT WEST CHESTER

A total of 76 ascospore traps were set on trees 4 to 8 inches in diameter, in a badly diseased coppice growth of native chestnut. Trees were selected so as to give varying conditions of the lesions, with perithecia in different stages of development. Some of the pustules showed perithecia which were just reaching maturity when the traps were set while others judging from the conditions of the pustules had probably expelled spores during the previous summer. The first traps (1–16) were set on November 26, 1912; a second lot (17–32) were placed December 3, 1912; another addition (33–36) was made December 18, 1912; and the number was further increased (37–49) on December 31, 1912. Nos. 1–49 inclusive were under continuous observation during all or part of the winter of 1912–13. During the spring several more traps (50–52) were set. A fence made of chestnut rails gave an opportunity to test ascospore expulsion under different conditions, and on May 1, 1913, traps (53–56) were placed over areas of perithecial pustules on several rails. The last traps (57–76) were set August 15, 1913. Nos. 50–76 included no perithecia that had reached maturity and expelled spores during the previous season (1912).

## THE RESULTS FROM THE TRAPS AT WEST CHESTER

From November 26, 1912 to March 19, 1913, there were 19 rain periods with precipitation varying from 0.01 to 1.8 inches, and maximum temperatures from 37° to 64° F. during the days of the rain, with no expulsion of ascospores (Table I). The first expulsion of ascospores for the season of 1913 occurred on March 20 following a rainfall of 1.64 inches and expulsion continued through the following months, but was checked by unfavorable temperatures early in November (Table II). From November 16, 1913 to May 4, 1914, there were 18 rain periods with precipitation varying from 0.10 to 1.95 inches and maximum temperatures from 34°–68° F. during the days of the rain, and no expulsion of spores. The first expulsion of ascospores for the season of 1914 occurred on May 5, following a rain of 0.71 inches (Table III). It may be noted that the first expulsion for 1914 was about six weeks later than in the spring of 1913. The records were continued to the end of July, 1914 (Table IV), when there was a forced discontinuance of the work.

TABLE I

*Ascospore Trap Tests, Records for West Chester, Pa., Winter and Spring, 1912–13*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Nov. 28 | 0.01 | 38 | 30 | 0 |
| Dec. 2 | 0.36 | 56 | 38 | 0 |
| " 4–6 | 0.5 | 68 | 36 | traces |
| " 11 | 0.03 | 43 | 37 | 0 |
| " 17–18 | 0.2 | 46 | 30 | 0 |
| " 19 | 0.89 | 53 | 33 | 0 |
| " 24 | 9.5 (snow) | 34 | 25 | 0 |
| " 27 | 1.02 | 37 | 32 | 0 |
| " 30 | 1.8 | 46 | 36 | 0 |
| Jan. 3 | 0.93 | 58 | 37 | 0 |
| " 4 | 0.1 (snow) | 39 | 27 | 0 |
| " 7–8 | 0.78 | 60 | 36 | 0 |
| " 10 | 0.13 | 40 | 22 | 0 |
| " 11–12 | 0.24 | 59 | 32 | 0 |
| " 15–16 | 0.81 | 46 | 26 | 0 |
| " 17–18 | 0.31 | 57 | 33 | 0 |
| " 20 | 0.24 | 54 | 33 | 0 |
| " 23–27 | 0.88 | 57 | 28 | 0 |
| Feb. 12 | 0.15 | 35 | 15 | 0 |
| " 22 | 0.07 | 58 | 45 | 0 |
| " 27 | 0.78 | 60 | 38 | 0 |
| Mar. 10 | 0.53 | 49 | 38 | 0 |
| " 13–15 | 1.375 | 64 | 29 | 0 |
| " 20 | 1.64 | 63 | 49 | 47 |

TABLE II

*Ascospore Trap Tests, Records for West Chester, Pa., 1913*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Mar. 20 | 1.64 | 63 | 49 | 47 |
| “ 26–27 | 1.18 | 69 | 38 | 47 |
| Apr. 4 | 0.56 | 76 | 44 | 21.5 |
| “ 10–13 | 2.49 | 58 | 27 | 36.5 |
| “ 13–16 | 1.57 | 67 | 41 | 4 |
| “ 27–28 | 2.43 | 74 | 48 | 65.4 |
| “ 29 | 0.11 | 56 | 54 | 8 |
| May 16–17 | 0.65 | 80 | 48 | 46.4 |
| “ 21–24 | 3.24 | 77 | 46 | 70.3 |
| “ 27–28 | 0.69 | 72 | 53 | 83.3 |
| June 7 | 0.12 | 83 | 64 | 0 |
| “ 20 | 0.08 | 88 | 62 | 50 |
| “ 21 | 0.02 | 82 | 65 | 11.1 |
| “ 24 | 0.19 | 78 | 65 | 52 |
| “ 27–28 | 0.22 | 86 | 66 | 66 |
| July 5–6 | 0.16 | 92 | 69 | 28.8 |
| “ 9 | 0.30 | 75 | 56 | 47.1 |
| “ 12 | 0.75 | 86 | 56 | 88.5 |
| “ 17–18 | 0.20 | 87 | 57 | 27.5 |
| “ 21 | 0.05 | 82 | 61 | 4 |
| “ 24 | 0.04 | 88 | 66 | 4 |
| “ 28 | 0.06 | 91 | 70 | 0 |
| “ 29–30 | 0.74 | 96 | 68 | 60.8 |
| Aug. 1 | 0.05 | 83 | 72 | 11.5 |
| “ 6 | 1.98 | 83 | 62 | 74 |
| “ 10 | 0.37 | 93 | 72 | 75.5 |
| “ 18 | 0.03 | 93 | 70 | 0 |
| “ 19 | 0.40 | 80 | 62 | 67.6 |
| “ 22 | 0.25 | 76 | 50 | 63.4 |
| “ 27 | 0.175 | 85 | 63 | 50.7 |
| “ 29–30 | 1.10 | 81 | 62 | 74.6 |
| Sept. 7 | 0.37 | 86.5 | 66.5 | 62.8 |
| “ 13 | 0.095 | 70 | 58 | 18.5 |
| “ 17–18 | 0.26 | 74.5 | 52 | 57.7 |
| “ 18–19 | 0.68 | 74.5 | 58 | 62 |
| “ 19–20 | 0.09 | 65.5 | 57 | 34.2 |
| “ 20–22 | 1.26 | 79 | 48 | 77.1 |
| Oct. 1–3 | 1.30 | 71 | 52 | 54.3 |
| “ 11 | 0.73 | 69.5 | 62 | 67.1 |
| “ 19–20 | 0.86 | 69 | 50 | 64.3 |
| “ 20 | 0.08 | 69 | 54 | 2.8 |
| “ 24–26 | 1.44 | 64 | 49 | 74.3 |
| Nov. 8–9 | 1.00 | 60 | 37 | 54.3 |

The percentage of traps showing expulsion for any rain period during the season of perithecial activity varied from 0 to 88.5 (Tables I–IV). The failure to get expulsion of spores from all traps depended on the following conditions:

1. Temperature below the optimum for expulsion.
2. Insufficient rainfall.
3. Location of the trap with reference to the direction of the rain.
4. Condition of the perithecia (not in proper stage to expel spores).

TABLE III

*Ascospore Trap Tests, Records for West Chester, Pa., Winter and Spring, 1913–14*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Nov. 8–9 | 1.00 | 60 | 37 | 54.3 |
| " 15–16 | 0.96 | 58 | 28 | 0 |
| " 28 | 0.62 | 44.5 | 33.5 | 0 |
| Dec. 7 | 0.53 | 52 | 41 | 0 |
| " 21 | 0.05 | 47 | 27 | 0 |
| " 23–5 | 1.95 | 50 | 32 | 0 |
| Jan. 3–5 | | 39 | 25 | 0 |
| " 24 | 1.35 | 50 | 40 | 0 |
| " 31 | 0.88 | 63 | 36 | 0 |
| Feb. 6–7 | 0.62 | 48 | 27 | 0 |
| " 13–14 | 4.5 (snow) | 32 | 0 | 0 |
| " 16 | 1.5 " | 25 | 2 | 0 |
| " 19 | 0.68 | 34 | 29 | 0 |
| Mar. 1–2 | 4.50 (snow) | 38 | 15 | 0 |
| " 5–6 | 6.00 " | 33 | 29 | 0 |
| " 11 | traces " | 29 | 20 | 0 |
| " 18 | 0.10 | 43 | 29 | 0 |
| " 20–22 | 3.5 (snow) | 34 | 11 | 0 |
| " 28 | 0.35 | 58 | 37 | 0 |
| April 1 | 0.25 | 48 | 37 | 0 |
| " 8 | 0.60 | 67 | 41 | 0 |
| " 15 | 0.49 | 45 | 41 | 0 |
| " 20 | 0.44 | 68 | 45 | 0 |
| " 25 | 1.57 | 50 | 44 | 0 |
| " 30 | 0.10 | 50 | 45 | 0 |
| May 5 | 0.71 | 65 | 59 | 11.8 |

There was a marked example of the influence of the temperature following a rain of 1.57 inches on April 13–16, 1913, when only 4 percent of the traps showed expulsion. The maximum rainfall following which there was no expulsion of ascospores when temperature conditions were favorable was 0.12 inches on June 7, 1913. A small percentage of traps sometimes showed expulsion when the rainfall was less than 0.12 inches. (See Tables I–IV.) The number of rains for the entire period covered by our investigations following which there was expulsion of ascospores is shown in Table V.

Perithecial activity in 1913 began in the spring as soon as temperature conditions became favorable, but since the temperatures at this

### TABLE IV

*Ascospore Trap Tests, Records for West Chester, Pa., Spring and Summer, 1914*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| May 5 | 0.71 | 65 | 59 | 11.8 |
| " 8 | 0.21 | 58 | 52 | traces |
| " 12 | 0.56 | 72 | 45 | " |
| " 27 | 0.19 | 92 | 65 | 3 |
| June 4 | 0.30 | 70 | 61.5 | 9.2 |
| " 14–15 | 0.08 | 75.5 | 58 | 0 |
| " 21–22 | 1.08 | 80 | 48 | 26.1 |
| " 27 | 0.68 | 86 | 60 | 29.2 |
| July 2 | 1.15 | 82 | 64 | 24.6 |
| " 5 | 0.35 | 73 | 61 | 34.3 |
| " 7 | 0.70 | 70 | 59 | 31.1 |
| " 13–15 | 3.14 | 85 | 66 | 36.6 |
| " 16 | 0.25 | 83 | 69 | 40 |
| " 25 | 0.31 | | | 16.6 |
| " 28 | 3.58 | | | 33.3 |

### TABLE V

*Summary of Number of Rain Periods and Number of Times Spores Were Expelled*

| Period | No. of Rain Periods | Amount of Rain in Inches | No. of Rains During Which Expulsion Occurred |
|---|---|---|---|
| Nov. 26, 1912–Mar. 19, 1913 | 19 | 12.125 | 0 |
| Mar. 20, 1913–Nov. 15, 1913 | 42 | 30.01 | 39 |
| Nov. 16, 1913–May 4, 1914 | 18 | 11.64 | 0 |
| May 5, 1914–July 31, 1914 | 15 | 13.04 | 14 |

### TABLE VI

*Records for Ascospore Traps, Martic Forge, Pa., Winter of 1912–13*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Jan. 29 | .08 | 38 | 31 | 0 |
| " 31 | .06 | 62 | 42 | 0 |
| Feb. 4 | .70 | 37 | 28 | 0 |
| " 10 | .03 | 32 | 18 | 0 |
| " 17 | .04 | 35 | 29 | 0 |
| " 22 | .09 | 56 | 49 | 0 |
| " 27 | .36 | 58 | 38 | 0 |
| Mar. 5 | .02 | 45 | 31 | 0 |
| " 10 | .55 | 52 | 41 | 0 |
| " 13 | .10 | 55 | 53 | 0 |
| " 14 | 1.29 | 67 | 53 | 2 |

time were generally below the optimum for spore expulsion, the highest activity was not reached until the month of May. There was a decline in spore expulsion during the months of June and July, but there was abundant expulsion in August, September and October. In November, with the return of unfavorable temperatures, the perithecia ceased to expel spores. This seasonal relation is represented graphically in Fig. 2.

TABLE VII

*Records for Ascospore Traps, Martic Forge, Pa., Spring and Summer, 1913*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Mar. 14 | 1.29 | 67 | 53 | 2.0 |
| " 15 | .92 | 61 | 56 | 6.0 |
| " 20 | .62 | 66 | 49 | 6.0 |
| " 21 | .03 | 68 | 52 | 0 |
| " 26–27 | 3.47 | 65 | 30 | 68.0 |
| " 31 | .04 | 69 | 49 | 0 |
| Apr. 3 | .10 | 74 | 39 | 0 |
| " 5 | .23 | 59 | 40 | 19.6 |
| " 14 | 1.78 | 57 | 51 | 65.3 |
| " 16 | 1.15 | 59 | 45 | 0 |
| " 28 | 2.33 | 58 | 45 | 98.0 |
| " 29 | .07 | 49 | 35 | 4.0 |
| May 15 | .11 | 74 | 42 | 2.0 |
| " 16–17 | .74 | 84 | 49 | 98.0 |
| " 21 | .27 | 64 | 50 | 58.0 |
| " 29–30 | .69 | 75 | 44 | 95.0 |
| June 19–21 | .34 | 92 | 52 | 88.0 |
| " 23 | .26 | 75 | 61 | 96.0 |
| " 27 | .37 | 101 | 77 | 100.0 |
| July 2 and 5 | 1.97 | 97 | 66 | 100.0 |
| " 9 | .59 | 69 | 63 | 100.0 |
| " 17 and 20 | .13 | 89 | 57 | 96.0 |
| Aug. 1 | 2.68 | 87 | 68 | 100.0 |
| " 6 | 1.37 | 82 | 64 | 98.0 |
| " 10 | 1.13 | 97 | 70 | 98.0 |
| " 22 | .17 | 73 | 58 | 100.0 |
| " 29 | .30 | 79 | 68 | 100.0 |
| Sept. 7 | .67 | 92 | 69 | 86.0 |
| " 12 | .09 | 67 | 56 | 68.0 |
| " 17–18 | .19 | 75 | 54 | 82.0 |
| " 20–21 | 2.37 | 80 | 57 | 92.0 |
| " 29 | .02 | 68 | 55 | 0 |
| Sept. 30–Oct. 2 | 1.63 | 77 | 50 | 100.0 |
| Oct. 11 | .67 | 68 | 56 | 94.7 |
| " 19 | 1.05 | 57 | 46 | 85.0 |
| " 20 | .15 | 68 | 42 | 1.4 |
| " 25–26 | 1.04 | 61 | 50 | 93.3 |
| Nov. 8–9 | .91 | 58 | 33 | 83.3 |
| " 15–16 | .83 | 40 | 25 | 0 |

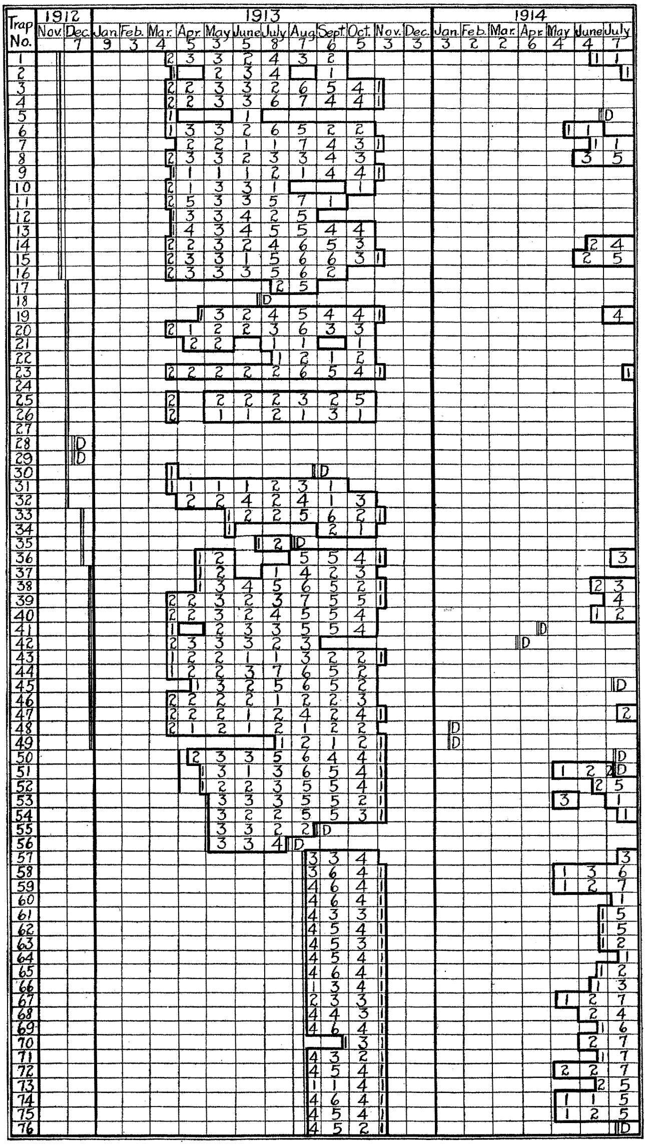

FIG. 3. Chart showing the seasonal duration of ascospore expulsion at West Chester, Pa. The vertical parallel lines indicate the approximate time when the traps were set. D following two parallel lines indicates the discontinuance of a trap. The figures below each month refer to the number of rain periods for the month, while the figures opposite each trap number represent the number of rain periods for the month following which there was an expulsion of ascospores.

At the beginning of our work it was an open question as to whether perithecial pustules would exhaust their power to expel spores during the course of a single season. Our records show that bark bearing stromata with perithecia that probably were active during the season of 1912, gave an abundant expulsion during the season of 1913 (Traps 1–49). For these same traps there was either no expulsion or it was irregular and spasmodic during the season of 1914. Somewhat more certain evidence of the continuation of perithecial activity during two seasons is shown by the records for traps 57–75 from which there was an abundant spore expulsion during the season of 1913 and the part of the season of 1914 covered by our observations. This duration of ascospore expulsion from the different traps and also their seasonal activity is represented in an accompanying chart (Fig. 3).

Records were obtained on the majority of the 76 traps for the entire period covered in this report. Sixteen traps were discontinued before the expiration of the work for various reasons. In 9 cases the bark was shed from the tree due to the action of blight and accessory agencies, in 4 the bark was overgrown by sporophores of sap rot fungi, while one was overrun by a foreign mycelium.

## THE TRAPS AT MARTIC FORGE

A total of 75 ascospore traps were set in the chestnut orchard at Martic Forge on Paragon trees ranging from 3 to 12 inches in diameter. The pustules over which the traps were placed were in varying stages of development, but were on the whole much younger than those at West Chester.

The first traps (1–41) were set on January 21–24, 1913; four (42–45) were added on January 31; three (46–48) on February 10; and two more (49–50) on February 12. An addition of twenty-five traps (51–75) was made early in October 1913, and the first record on these was taken for the rain of October 11. These last 25 traps were placed over pustules which had just reached sufficient maturity to expel spores during the season of 1913.

## THE RESULTS FROM THE TRAPS AT MARTIC FORGE

There were 10 rain periods between January 29 and March 13, 1913, with a precipitation ranging from 0.02 to 0.70 inches (Table VI). No expulsion of ascospores occurred during this period. Temperatures favorable for perithecial activity were first offered on March 14, 1913, when 2 percent of the traps shot spores following a rain of 1.29 inches. From March 14 to November 9 there were 38 rain periods with precipitation varying from 0.02 to 3.47 inches (Table VII). During most of these rain periods there was abundant expulsion of ascospores, and following seven of them all of the traps expelled spores. After November 9 the temperatures were again unfavorable for perithecial activity, and no expulsion occurred for any of the 21 rains between November 10, 1913 and April 15, 1914 (Table VIII). Beginning with April 20, with the return of higher temperatures, there was again an abundance of expulsion following every rain period until July 31, 1914, when the work was discontinued (Table IX).

Table VIII

*Records for Ascospore Traps, Martic Forge, Pa., Fall and Winter, 1913–14*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Nov. 8–9 | .91 | 58 | 33 | 83.3 |
| " 15–16 | .83 | 40 | 25 | 0 |
| " 27–29 | .54 | 49 | 32 | 0 |
| Dec. 1 | .06 | 44 | 33 | 0 |
| " 7 | .51 | 52 | 37 | 0 |
| " 21 | .13 | 49 | 26 | 0 |
| " 23–25 | 2.25 | 49 | 28 | 0 |
| Jan. 3–5 | 2.11 | 41 | 25 | 0 |
| " 24 | 1.21 | 47 | 39 | 0 |
| " 31 | .83 | 61 | 34 | 0 |
| Feb. 6–7 | .48 | 46 | 24 | 0 |
| " 13–14 | 1.12 | 30 | 3(?) | 0 |
| " 19 | .62 | 31 | 26 | 0 |
| Feb. 28–Mar. 1 | .38 | 40 | 18 | 0 |
| Mar. 5–6 | .72 | 36 | 17 | 0 |
| " 11 | .03 | 30 | 18 | 0 |
| " 20–22 | .34 | 37 | 17 | 0 |
| " 28 | .36 | 59 | 36 | 0 |
| Apr. 1 | .28 | 45 | 35 | 0 |
| " 8 | .59 | 65 | 35 | 0 |
| " 11 | .07 | 59 | 33 | 0 |
| " 15 | .70 | 45 | 39 | 0 |
| " 20 | .59 | 67 | 53 | 10.8 |

It will be noted (Tables I and VI) that in the spring of 1913 expulsion began at Martic Forge a few days earlier than at West Chester. In the fall of 1913 perithecial activity ceased with the same rain period at both places, but in the following spring the Martic Forge traps were again the first to expel spores. There was very little difference between the temperatures at the two stations. The earlier start at Martic Forge is accounted for by the fact that the pustules over which the traps were set were on the whole much younger and in better condition to expel spores than those at West Chester. During the seasons of perithecial activity for both 1913 and 1914, a larger percentage of the traps at Martic Forge expelled spores than at West Chester. Furthermore a much more copious expulsion was obtained from individual traps at Martic Forge.

TABLE IX

*Records for Ascospore Traps, Martic Forge, Pa., Spring and Summer, 1914*

| Rainfall | | Temperature | | Percentage of Traps Showing Expulsion |
|---|---|---|---|---|
| Date | Amount, Inches | Max. | Min. | |
| Apr. 20 | .59 | 67 | 53 | 10.8 |
| " 25–26 | 1.57 | 68 | 44 | 2.7 |
| May 5 | 1.11 | 66 | 60 | 27.0 |
| " 8 | .13 | 62 | 50 | 32.9 |
| " 12 | .40 | 81 | 47 | 16.2 |
| " 28 | .42 | 87 | 60 | 5.6 |
| June 4 | .42 | 72 | 64 | 46.6 |
| " 8 | .22 | 97 | 65 | 20.8 |
| " 18 and 21–23 | .97 | 91 | 50 | 43.1 |
| " 23–25 and 28 | 2.10 | 94 | 62 | 68.6 |
| July 2–3 | 1.63 | 80 | 54 | 55.6 |
| " 4–5 | .28 | 73 | 57 | 78.1 |
| " 10 and 12 | .95 | 90 | 66 | 69.2 |
| " 13–14 | .23 | 84 | 65 | 69.9 |
| " 14–15 | .53 | 86 | 66 | 75.3 |
| " 15–16 | 2.31 | 86 | 66 | 53.4 |
| " 24–25 | 1.17 | 91 | 67 | 45.8 |
| " 28 | 2.61 | 81 | 55 | 56.2 |

TABLE X

*Summary of the Number of Rain Periods and Number of Times Spores were Expelled at Martic Forge, Pa.*

| Period | No. of Rain Periods | Amount of Rain in Inches | No. of Rains During which Expulsion Occurred |
|---|---|---|---|
| Jan. 29, 1913–Mar. 13, 1913 | 10 | 2.03 | 0 |
| Mar. 14, 1913–Nov. 9, 1913 | 38 | 31.94 | 33 |
| Nov. 10, 1913–Apr. 19, 1914 | 23 | 14.16 | 0 |
| Apr. 20, 1914–July 31, 1914 | 18 | 17.64 | 18 |

Under laboratory conditions the minimum temperature for ascospore expulsion was found to be between 50 and 55° F. While it was impossible to get the maximum and minimum temperatures for the exact period during which ascospores were expelled after each rain, still the maximum and minimum temperatures during each rain period (Tables VI–X) show that the minimum temperature for expulsion in the field corresponded quite closely with that in the laboratory. The rain of April 14, 1913, offers a good example of a heavy rain with no expulsion, due to low temperatures (Table VII). Although copious expulsion occurred both before and after this date, and the precipitation had been heavy (1.15 in.), the temperatures were below the minimum for perithecial activity.

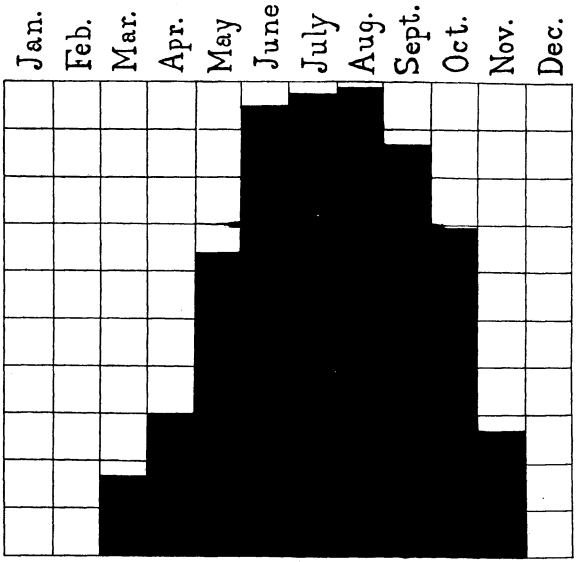

FIG. 4. Diagram showing the relative intensity of ascospore expulsion at Martic Forge, Pa., during the season of 1913.

The number of rains for the entire period covered by our investigations and the number of rains following which ascospore expulsion took place, are shown in Table X.

The seasonal relation of expulsion at Martic Forge for the year 1913 was somewhat different from that at West Chester. At the latter place the monthly percentage of traps showing expulsion increased suddenly from March to a maximum in May; during June and July there was a decided decrease, but after July there was abundant expulsion until November (Fig. 2). At Martic Forge there

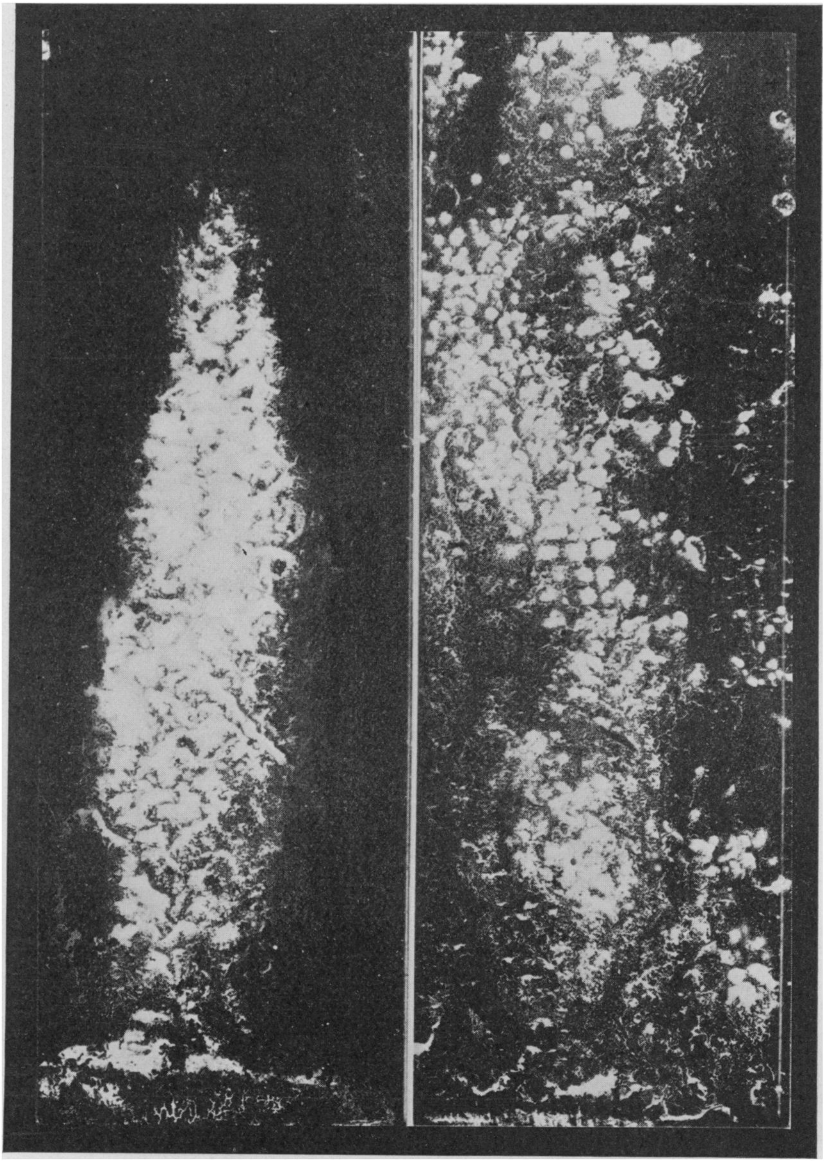

FIG. 5. Photographs of slides from trap 52 (upper) and trap 62 (lower). Slide from 52 was taken following a rain of 1.63 inches on July 2–3, 1914; slide 62 following a rain of 0.95 inches on July 10–12, 1914.

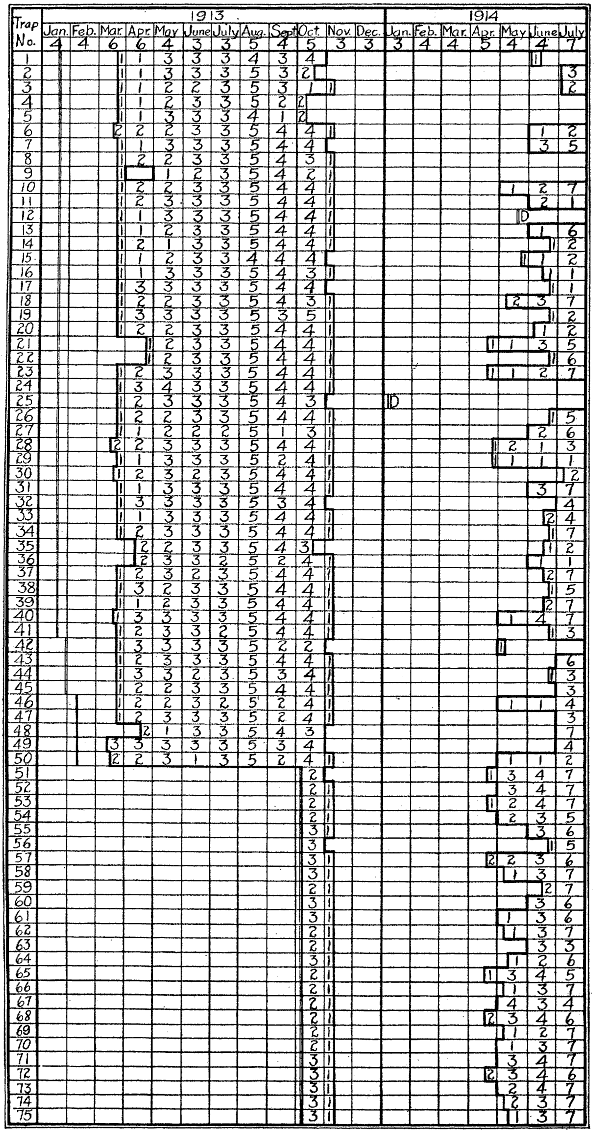

FIG. 6. Chart showing the seasonal duration of ascospore expulsion at Martic Forge, Pa. (See legend of Fig. 3 for more detailed explanation.)

was a gradual increase from the beginning of expulsion in March to a maximum in August, followed by a more sudden, though steady, decrease until November (Fig. 4). The maximum at Martic Forge (98.8 percent) was also much higher than that at West Chester (67.3 percent). It is difficult to explain this seasonal difference except to suppose that it might have been due to the difference already mentioned in the condition of the pustules.

TABLE XI

*Record of Expulsion from Typical Young and Mature Pustules at Martic Forge for the Active Season, 1913*

| Rainfall | | Trap Numbers and No. of Active Ostioles | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Date | Amount, Inches | Young Pustules | | | | Mature Pustules | | | |
| | | 21 | 23 | 37 | 40 | 11 | 17 | 28 | 43 |
| Mar. 15........ | .92 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 |
| " 20........ | .62 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| " 26–27..... | 3.47 | 0 | N | 14 | 0 | 15 | 8 | N | 28 |
| Apr. 3........ | .10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| " 5........ | .23 | 0 | 0 | 0 | 27 | 0 | 1 | 0 | 0 |
| " 14........ | 1.78 | 0 | N | P | P | 31 | N | 1 | 27 |
| " 16........ | 1.15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| " 28........ | 2.33 | 2 | N | N | 19 | N | N | 100 | N |
| May 15........ | .11 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| " 16–17..... | .74 | 25 | N | N | N | N | N | N | N |
| " 21........ | .27 | 0 | 1 | 0 | 1 | 14 | 16 | 21 | N |
| " 29–30..... | .69 | N | N | 64 | N | N | N | N | 11 |
| June 19–21..... | .34 | P | P | 0 | 95 | N | N | 1 | 7 |
| " 23........ | .26 | N | N | 6 | N | N | N | N | N |
| " 27........ | .37 | N | 13 | N | N | N | N | N | N |
| July 2 and 5... | 1.97 | 100 | 58 | 100 | N | N | N | N | 73 |
| " 9........ | .59 | N | N | 100 | N | 70 | 50 | N | 50 |
| " 17 and 20.. | .13 | 18 | 4 | 1 | 5 | 2 | 41 | 6 | 2 |
| Aug. 1........ | 2.68 | N | N | 47 | N | 48 | P | P | 54 |
| " 6........ | 1.37 | N | 32 | 38 | 36 | 22 | 18 | 8 | 65 |
| " 10........ | 1.13 | 35 | N | N | 40 | 26 | 24 | 18 | 27 |
| " 22........ | .17 | 22 | 66 | 4 | 33 | 34 | 22 | 11 | 21 |
| " 29........ | .30 | N | 43 | 4 | 49 | 37 | 27 | 15 | 20 |
| Sept. 7........ | .67 | N | N | 29 | 37 | 10 | 5 | 24 | N |
| " 12........ | .09 | N | 18 | 5 | 19 | 4 | P | P | 5 |
| " 17–18..... | .19 | N | N | 3 | 27 | 23 | P | 7 | P |
| " 20–21..... | 2.37 | N | N | N | N | 17 | P | 5 | 33 |
| " 30–Oct. 2.. | 1.63 | N | N | N | N | 14 | 6 | P | 34 |
| Oct. 11........ | .67 | N | N | N | N | 17 | 5 | 11 | 26 |
| " 19........ | 1.05 | N | N | N | 26 | 13 | 27 | 3 | 5 |
| " 20........ | .15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| " 25–26..... | 1.04 | N | N | N | N | 15 | 2 | 9 | 8 |
| Nov. 8–9...... | .91 | N | 65 | N | N | 19 | 0 | 10 | 8 |
| " 15–16..... | .83 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

N = numerous.

The fact that perithecial pustules would not exhaust their power to expel spores in the course of a single season is even more clearly shown by the traps at Martic Forge than by those at West Chester. Pustules tested by traps 1–50 must have expelled spores during 1912, before the traps were set. All of these traps showed active ostioles during 1913, and all but five of them expelled some spores during 1914. Pustules tested by traps 51–75 probably expelled their first spores during the spring and summer of 1913. All of these showed perithecial activity during 1914, most of them expelling spores in large numbers. Fig. 5 represents slides taken from traps 52 and 62 during July, 1914, and shows how copious the expulsion may be during the second season. No heavier shooting was obtained from any of the traps even during their first season of activity.

The accompanying chart (Fig. 6) represents the duration of expulsion and the seasonal activity for the traps at Martic Forge.

In some instances the tree was entirely dead and the bark peeling off at the time the trap was set, early in 1913. Nearly all of these cases showed continued perithecial activity during 1913, and most of them had not entirely lost their power to eject spores in 1914. This is best shown by traps 10, 43 and 50 (Fig. 6).

There is a difference between the continued activity of young and mature pustules. The former continue to shoot spores unabated throughout the entire season, whereas the maturer pustules eject a larger number of spores during the early part of the season and show a gradual decline toward the winter months. In Table XI is presented the record of expulsion of ascospores for each rain period during the active season of 1913 for typical young and mature pustules.

## EXPULSION OF ASCOSPORES FROM BARK SHED FROM OLD INFECTIONS

Trap 41 at West Chester was discontinued in April, 1914, the bark to which the trap was attached being shed from the tree. In order to determine whether perithecia in bark shed from trees would continue to expel spores, five representative pieces from bark collected on the ground beneath trap 41 were brought to the laboratory and tested for ascospore expulsion. Each of the pieces (1 × 3 inches) showed active ostioles, the maximum number for any day during the progress of the test being forty. This activity was less than from similar bark taken directly from cankers. Bark shed from the rail fence adjacent to traps 53 and 54 was also tested for spore expulsion with positive results. These results give added emphasis to the statement already made (7) that the chestnut blight fungus has a most remarkable power of ascospore production.

## Discussion

A comparison of the results obtained at the two stations shows a very general agreement in the more important features. All of the traps at West Chester were set on native coppice while those at Martic Forge were on Paragon trees grafted on native coppice. Some of the traps at the latter station were set below the graft unions. The greater activity of the perithecia during the second season at Martic Forge as compared with the results at West Chester is probably due to the host relation, permitting a somewhat more rapid maturing of the fungus at the latter place.

Since the prolonged perithecial activity established by our observations for *Endothia parasitica,* is not in accord with what is known in regard to many other pyrenomycetous fungi, an explanation for this peculiarity should be sought. There seem to be two important features in the development of the fungus that contribute to prolonged perithecial activity. First, the period of successive maturing of asci is very extended. This fact is substantiated by the work of Heald and Walton (7) on the expulsion of ascospores under laboratory conditions, and is in agreement with the study by Anderson (9) of the morphology of the perithecia. The second feature not so clearly revealed by the morphological studies (9) appears to be the successive maturity of the perithecia in a given stroma. All perithecia in a given stroma do not reach maturity at the same time, some being still buried deep in the stromata when the necks of others adjacent have reached the surface and are in a condition to expel spores. Add to the above features the fact that there is no seasonal relation to the maturing of perithecia and one must admit that *Endothia parasitica* is remarkably well equipped for the continuous production of ascospores.

During the progress of our work detailed examinations were made of the perithecial pustules included under each trap, their condition being recorded at the beginning of the tests and at intervals thereafter. As a result it can be definitely stated that the development of new stromata was the exception, the bulk of all expulsion recorded coming from stromata that were present at the beginning of the tests.

## SUMMARY

1. Expulsion of spores from the perithecia of *Endothia parasitica* begins in the spring with the first warm rains, and increases to a maximum of activity as conditions become more favorable, to be followed by a decline in the fall when lower temperatures prevail, and ceases entirely during the cooler portions of the year, although there may be an abundant rainfall. During 1913 the period of expulsion extended from about the middle of March to the middle of November. For 1912–13 there were 19 rain periods during the fall, winter and spring with no expulsion of ascospores, and in 1913–14 there were 18 rains which induced no expulsion of ascospores. During one third to one half of the year there is then no expulsion of ascospores, but during the remainder there is an abundant expulsion with each rain of any consequence (0.10+) except in a few instances when the temperature drops below the minimum.

2. Perithecial pustules of the chestnut blight fungus show a remarkable power of spore production. This power is not exhausted during the course of a single season, and in many cases is as marked during the second season as during the first. Our results point also to the conclusion that pustules first producing mature perithecia in the fall may continue to be a source of spores during the two following seasons of perithecial activity, the maximum of production occurring during the season following their maturity, with a gradually diminishing production of spores during the next season. This remarkable power is due to successive maturity of asci, to successive maturing of perithecia, and the successive maturing of stromata throughout the season.

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